THE TROUBLES OF BEING FEMALE: INVESTIGATING THE RELATIONSHIP BETWEEN SOCIAL STATUS AND STRESS LEVEL IN A POPULATION OF ADULT FEMALE YELLOW BABOONS IN AMBOSELI, KENYA

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Abstract:

The famous Whitehall studies of the social determinants of health suggest that low social status has a negative effect on a person's health due to a high level of chronic stress. Glucocorticoid hormone (GC) is released in the body as a direct response to stress, and is involved in important anti-inflammation and immunosuppression reactions that allow quick responses to stressful stimuli. For this reason, persistent and high levels of GC resulting from prolonged stress are thought to confer lower fitness by inhibiting immunity, producing a lower quality of life, and causing shorter longevity. There are many other examples of low dominance rank conferring lower fitness in animals, but this effect is species-dependent because subordinate animals can retain benefits as well. Thus, it is scientifically interesting to determine the direction of this effect in primate species. This study aimed to discover the relationship between social rank and stress in the adult female population of yellow baboons in the Amboseli Basin of Kenya. A previous study of male Amboseli baboons found that, with one exception, there is a negative relationship between high male rank and stress level. This information helped lead to the hypothesis that there is a negative correlation between high female rank and stress level. To test this hypothesis, the analysis used longitudinal data from over 12,000 samples collected over a 13-year period (2000-2013) from 191 adult females. Generalized Linear Mixed Models (GLMMs) were used to predict the effect of social rank on stress, as measured by fecal glucocorticoid concentrations. Other factors such as age, reproductive status, and environmental conditions were entered into the models as fixed effects and individual female identities were entered as a random factor. The results showed no significant relationship between a female's numerical rank and her stress level. Instead, it was determined that a female's proportional, or relative, rank affects her stress such that lower ranking individuals have higher stress. Though the final results supported the initial hypothesis, the insignificance of numerical rank was surprising.

Introduction:

The study of wild primate populations gives us insight that the study of laboratory model populations cannot. Because primate behavior and physiological systems closely resemble our own, understanding them provides us with an evolutionary perspective on our own current condition. The Amboseli Baboon Research Project has dedicated over 40 years of work to a specific primate species, the yellow baboon, *Papio cynocephalus* ("Amboseli Baboon Research Project" 2015). Through the years, the project continues to amass longitudinal data on every aspect of the baboons under study—from birthdates, to consortships, to gastrointestinal biome compositions, and beyond. Included in this wealth of data are steroid hormone measures, including testosterone, progestin, estrogen, and glucocorticoids (a type of cortisol). These hormonal records allow us to investigate the way in which yellow baboons physiologically respond to their environment (otherwise described as behavioral endocrinology). My investigation specifically studied the interaction between an adult female baboon's cortisol levels and her social status.

The importance of finding predictors for stress lies in the psychological and physiological consequences that stress can have on an organism. These consequences, in turn, can ultimately confer lower fitness on this organism. There is already a strong literature that supports dominance rank as a predictor of stress, and Sapolsky may be the most preeminent researcher contributing to this literature. His review found correlations between low rank and low fitness in many animals including rats, mice, and baboons (Sapolsky, 2004). This pattern was initially thought to describe all subordinate animals (Holst, 1998), but this view was complicated by evidence of some species where higher-ranking organisms did not necessarily have lower stress levels than lower-ranking ones. Creel (2001) surveyed a wide range of cooperatively breeding species including birds, primates, dogs, mongooses, wolves, and rodents. He found that for free-range species, dominants rarely had significantly lower stress levels than subordinates (Creel, 2001). Abbott et al. (2003) found inconsistencies between which group, dominant or subordinate, had higher stress across primates species. Their study included macaques, olive baboons, and squirrel monkeys, among others (Abbott et al., 2003). The reason for these discrepancies involves the concept of allostatic load. Allostatic load is the maintenance of homeostasis in an organism; it is mediated by hormones, mainly glucocorticoid (GC), and includes the entirety of the physical burden and thus energy demand on an individual's body (Goymann & Wingfield, 2004). The social composition of a species group can affect the allostatic load of its' individuals, so it may be that there are costs to higher rank. There is a direct example of this found in Amboseli male baboons. The alpha male is as stressed as his lower ranked counterparts, but the beta has decreased stress (Gesquiere et al., 2011). It is equally likely that, as both Sapolsky (2004) and Abbott et al. (2003) discuss, subordinate groups have available coping strategies that assuage the otherwise detrimental strains of stress—such as social support or outlets for frustration. Taken together, these complications mean that it is necessary to determine the significance of rank on stress and fitness for an individual species before drawing any conclusions. Further, ranking systems can be sex-specific within species, (Sapolsky, 2005). One could take female-dominant hyenas as an example of this. But a more pertinent example is Amboseli yellow baboons, whose rank and sex differences will be discussed in detail shortly. This calls for an even higher degree of discernment in studies that characterize the relationships between rank, stress, and fitness.

Stress consequences on the body, particularly those as a direct result of GCs, related hormones and feedback reactions, are fully characterized in the literature (Sapolsky et al., 2000). But communicating the full extent of their results goes beyond the scope of this introduction. Because my intent is to make the reader aware of the far-reaching costs of elevated stress levels, I will summarize a few key points of a review prepared by Sapolsky (2004) in order to emphasize the palpable effects of stress, which overlay the actions of GC. It should be noted that Sapolsky (2004) assumes a general underlying trend of low rank indicating high stress.

- There is a direct relationship between the psychological stressors and the physical consequences of low rank. Psychological stressors of a subordinate (or any stressed individual) involve:
    - Lack of predictability in their environments. A rat who does not know when an electric shock will come will be much more stressed than a rat receiving the same shock but does know that it's coming.
    - Lack of a sense of control. A rat that is trained in punishment avoidance and can try to avoid a shock is less stressed when the shock hits because he thinks he has the ability to evade it.
    - Lack of outlets for aggression. Distractions and the ability to displace aggression onto another individual reduces the stress response.
    - Personal interpretation of the stressor. For example, a rat that receives painful shocks that decrease in the amount of pain at every round will interpret the series of events more positively than a rat receiving increasingly painful shocks. The first rat will have lower stress levels than the second.

    - Lack of social support. “Numerous studies demonstrate the capacity of social support to blunt the stress-response in the face of numerous homeostatic challenges.” (Sapolsky, 2004)

- Physical stressors include a higher chance of being targeted for unprovoked aggression as higher ranked animals displace their stress; being at higher risk of predation since subordinates are forced into the periphery (Hamilton, 1971); as well as less access to food, for either they eat less or have to work harder to attain it. These consequences are related to the lack of predictability and lack of control described above. In addition, there is the physical absence of peers to have beneficial interactions with, as well as individuals ranked below them to take out their aggressions on.
- The resulting manifestations of stress that can confer lower fitness fall across four main regions of the body. Whether or not they are attributed directly to rank, these systems all involve interactions due to a higher level of glucocorticoids:
    - Endocrine system. Chronically higher levels of basal glucocorticoids (GC) have the opposite effect of the adaptive flight-or-fight response that is associated with short spikes in GC level. The response is designed such that when an organism’s peripheral nervous system (mammal, primate, etc.) encounters an environmental stressor, adrenal glands release GC into the bloodstream. The amount released is directly and positively related to the amount of stress that the animal is confronted with. Thus measure of GC is a reliable indicator of an animal’s stress level. GC acts to

suppress all non-vital functions like digestion, anti-inflammation reactions, and lymphatic system responses by blocking the normal feedback receptors of each so that the organism can efficiently respond to the situation it's confronted with. However, hyperactive basal levels of GC (hyperactive essentially meaning that the stress response is more "on" instead of "off") lead to blunted feedback responses. This means that the brain, pituitary, and adrenals are altered to be less sensitive to GC level changes. Thus, the organism now has a "sluggish" system, which means the brain is slow to signal the body to inactivate GC release after the stressor is removed. Interestingly, subordinate baboons in this state have identical processes to the ones seen in humans with major depressive disorder.

- Cardiovascular system. Instances of stress cause a rise in blood pressure and heart rate, these are unsurprising effects that most of us are familiar with. However, the stress response also causes the circulation of lipids and the decrease of HDL (good) cholesterol in the body. In addition to this, release of GCs affects normal estrogen levels, which would otherwise help to heal blood vessel damage, by suppressing them (done because the stress response diverts resources away from the non-vital reproductive system). There is evidence of decreased cardiovascular function and risk of disease in subordinate Old World monkeys, which is especially relevant, since yellow baboons belong to this taxon.

- Immune system. It is interesting to note that immunity is actually boosted in the first one to three hours of the stress response. This is due to stimulatory effects by GC on the lymphatic system, however, chronically high GC levels are again found to be costly. There is evidence to suggest that prolonged GC levels cause basal suppression of the immune system and lead to a greater risk of infectious disease.
- Reproductive System. There are negative effects on the reproductive system from high GC, prolactin, and beta-endorphins (the latter two are involved in the stress response along with GC). Increased stress hormones suppress secretion of gonadal hormones, thereby effectively decreasing gonadal function. In males, lower testosterone in subordinates has not been found to incur lower fertility as a direct result of stress (more on that later), but there is evidence for suppressed gonad function producing lower fertility in females. This is attributed to four possible mechanisms: “"social contraception" (i.e., direct stressful harassment by dominant animals), fewer calories, more work required for calories (this aspect further supported by work done later (Habig & Archie, 2015)), and constitutional biology giving rise to both lower rank and impaired gonadal function.” (Sapolsky, 2004) There has been evidence found for all four of these mechanisms in females.

Even though the debilitating effects of stress on a primate’s longevity and fitness should now be clear, the fact that dominance does not always mean lower basal glucocorticoid levels should still be kept in mind; this necessitates further species-specific and sex-specific investigation. The relationship between stress, rank, and the reproductive system becomes nuanced when we turn our attention back to yellow baboons.

In Amboseli, yellow baboons live in multi-male, multi-female groups, have multiple mate pairs, and cooperatively breed. Male baboons disperse from their maternal groups and engage in physical combat to establish a linear social hierarchy. This hierarchy is dynamic and the exact numerical rank order may change from month to month. The effect that male hierarchy has on access to reproductive (and other) resources can be described using the “priority of access” model, in which a dominant male will have priority access to an available female over a subordinate (Altmann, 1962). This is important due to the fact that yellow baboons are year-long breeders, and cycle regularly, as humans do. This means females are not always ready to mate, nor do all females mate during the same season. It may be that only one or a few females are available at any one time. There are a number of ways that subordinate males may circumvent this system, through sneak copulation (rather self-explanatory), female choice, fighting for mating opportunites, “stealing” a female when the dominant male fails to guard her effectively (happens because guarding introduces a cost onto the male by infringing on foraging time (Alberts, 1996)), or by teaming up to overcome a dominant male. Even so, if both hierarchy composition and order remain stable then dominant males are going to receive the higher proportion of consort time with fertile females (Alberts et al., 2003). Further, evidence supporting the low rank-high stress relationship and the related endocrinological effects has been found in Amboseli males. As stated previously, a positive linear relationship between fecal glucocorticoid concentrations and numerical rank was found from the beta male to the lowest ranked male (it is important to remember that high rank is a low number) (Gesquiere et al., 2011). An additional study found increased cortisol in low ranked and/or socially isolated baboons (Sapolsky et al., 1997), while another found evidence of faster healing rates from both illness and injury in the alpha male along with evidence of immunosuppression among the lower ranks.

Finally, there are female yellow baboons. As mentioned, females breed year-round and engage in multiple matings. In contrast to male dispersal, females exhibit natal philopatry, meaning that they remain in their maternal groups for their entire lives. As a result, females interact with the same individuals for most part, except for instances of group fission or fusion. Further, female rank is passed down through matrilineal legacy, resulting in a nepotistic dominance hierarchy (Lea et al., 2014). A mother's daughters will rank directly below her and take her rank when she dies. While there is some variance, such as a female failing to achieve the rank below her mother, or one aggressively attaining a higher rank during her sub-adult years than she should have (Lea et al., 2014), for the most part a female's rank is life-long and stable. Further, even though the general pattern of low rank causing relative social isolation may occur, all females in a group will have a chance to mate so female rank is not directly correlated with reproductive success in the way that it is for males. (A low ranking male has a strong chance of not mating.) Preferential treatment by a female's peers is also not completely contingent on rank, it is more dependent on maternal kinship (Silk, Altmann, et al., 2006). Because these differences mean that females are expected to have different stressors than males, we should not generalize the findings in male yellow baboons to include females, though it is possible to perhaps infer some similarities. In light of this, this study set out to determine the relationship between female social rank and stress, and to test the hypothesis that lower-ranking females would have higher stress levels.

Material and Methods:

In this study, I tested the hypothesis that there is a negative relationship between female dominance rank and stress in an adult female population of yellow baboons in the Amboseli Basin of Kenya. To do this, I used fecal glucocorticoid concentrations (fGC) from over 12,000 fecal samples collected over a 13-year period, 2000-2013. These samples came from 191 adult females. Samples were processed in lab after standardized collection procedures in the field (Full protocols are available on the ABRP website ("Amboseli Baboon Research Project," 2015)) . Storage and extraction procedures then took place (Khan et al., 2002) and samples were then radioimmunoassayed for the glucocorticoid hormone (Gesquiere et al., 2008). Generalized Linear Mixed Models (GLMM) were then used to predict the effect of rank on fGC concentrations.

These types of models predict the effect of both fixed and random factors on a dependent variable. A fixed factor is characterized by the researcher's desire to determine how the mean of the dependent variable changes as that factor's value changes. Fixed factors for my model included female rank, age, pregnancy status, hot/cold season, and wet/dry season. Rank and age are continuous fixed factors, meaning the estimate the model provided is calculated from the mean differences between the dependent variable data points and those between the independent variable points. These differences are then compared by determining the "rise over run." Thus the resulting slope, or regression line, tells me how Y changes in response to X. Climatic variables and pregnancy status are binary, or categorical, fixed factors (it is either hot or cool outside; a female is either pregnant or is not.). For these, the model made a prediction based on the average change in the overall mean value of the dependent variable that is due to the factor (i.e., the average GC level of non-pregnant females and the average of GC levels of pregnant females). Female identity was entered as a random factor in order to account for the fact that I was not interested in idiosyncratic differences among individual females. Instead, I was interested in the systematic differences that were due to the different environmental factors females experience together.

I assessed two different measurements of dominance rank. The first is numerical, or ordinal rank. Ordinal rank is a set of integers that describe the group's hierarchy. Ordinal rank is the method most commonly used in Amboseli studies. Proportional rank is obtained by taking an individual's ordinal rank and dividing it by the total number of possible rankings (i.e. the total number of adult females in a specific group). So, if a female in group A has an ordinal rank 4, to find her proportional rank you take the total number of adult females in her group, perhaps 10, and divide, in this case to produce a proportional rank of 0.4. If she moved up to ordinal rank 3, then her proportional rank would be 0.3. It may seem superfluous to have to divide by the number of females, and this is why proportional rank is sometimes overlooked completely, however, it becomes more intuitively relevant when taking into account that female group size is widely variable. A different female in another group may also have an ordinal rank of 4, but she may live with only four other females. This means that while her ordinal rank remains the same as the female in the previous example, her proportional rank is 0.8 and is thus has a relatively lower rank. (Remember, colloquially we say that someone of a higher dominance rank has a lower numerical value). Measuring rank this way allows us to compare relative female statuses.

Data Analysis:

Longitudinal data for all adult females stored in the ABRP database was extracted for analysis. Names, ages, reproductive statuses, ranks, and glucocorticoid concentrations were pulled. Female fecal samples are collected in the field as often as desired, thus there is uneven sampling in individual female contribution. To mitigate this effect, a monthly average was calculated for the female age at time of sample as well as for the GC concentrations of all the samples taken in a given month. Monthly weather data was determined as well.

Fecal glucocorticoid concentrations were transformed by a logarithmic function in order to approach normality. I then used the lmer function in the R

Studio statistical package to construct generalized linear mixed models (GLMM) to predict the effect of both ordinal and proportional rank on fGC concentrations.

Results:

The results of the models comparing the effects of proportional rank on fecal glucocorticoid fGC levels supported the hypothesis that lower ranking females have higher stress. Females of a higher proportional rank had lower fGC levels than those of lower proportional rank.

For example, Model 3 (Table 3) shows the effects of proportional rank, dry season, hot temperature, pregnancy, and age on log fGC. The cell where the "Estimate" column intersects with the row "Proportional rank" indicates that, with all else held constant, every one unit increase in proportional rank is associated with a .0497 unit increase in log fGC concentration. We accept this as a good estimate because the standard error is small. Because standard error is the deviation of the variances of a sampled population, a small number tells us that our estimation does not greatly deviate from the real population mean (As a reminder all statistical tests are rooted in the idea that we are only sampling from the actual population). The standard error is in addition to the justification of our estimate by the p-value, which here indicates that there is less than 0.003 percent chance that our estimate came from the same population as the intercept (log fGC) population. This is well under the standard significance threshold p-value of 0.05.

The models found other significant fixed effects on stress as well. These were age, pregnancy, hot temperatures, and the dry season. I found that older females have more stress than younger females; pregnant females have considerably higher stress levels than non-pregnant ones; hotter temperatures increase female stress; and female stress is higher during the dry season. In contrast to these results, the models that compared ordinal rank showed no significant effect of ordinal rank on fGC concentrations. One model used ordinal rank alone, and the other used both ordinal and proportional rank. The inclusion of both measurements in one model provided greater support of the importance of proportional rank over ordinal rank, while this model showed a correlation between ordinal and proportional rank, there was still no significant relationship between ordinal rank and stress. Of course, correlation between the measurements was expected due to the necessity of ordinal rank in the calculation of proportional rank. Also, the similarity in values and estimates between models demonstrated repeatability in the results. Please see Appendix for related scatterplots and graphs.

Discussion:

My results suggest that the stress level of an adult female yellow baboon is affected by her relative status in a group. A female's dominance rank describes an individual's position among the adult females in her social group, it is also used to predict her ability to win conflicts and gain access to resources (Lea et al., 2014), which includes mating opportunities in some species (Barrett et al., 2002). Sometimes lower rank means that a female gives up her chance of reproduction in situations that are not affected by high GC at all (Abbott et al., 2003). In these cases, the subordinate females support rearing the dominant female's offspring. Though the simplest example of this is the role of female ants in eusocial ant colonies, there are also mammalian species in which this occurs (Sapolsky, 2005). Lower rank is related to social isolation as well, and studies have found that a smaller social network leads to shorter longevity (Sapolsky et al., 1997). For females in Amboseli, low rank can also mean that offspring are less likely to survive (Silk, Alberts, et al., 2006). Having high rank avoids all of these negative consequences.

A recent paper has found that injury risk in female yellow baboons is associated with her proportional rank (Archie et al., 2014). Surely, a heightened risk of injury relates to the psychological stressor of increased unpredictability discussed in the introduction that raises GC concentration. Thus the paper provides evidential support for the conclusions of this project. Archie et al. explained that females of similar proportional rank have the same risk of injury, independent of their dissimilar ordinal ranks, "a female ranked 5 in a small group experienced higher injury risk than a female ranked 5 in a large group" (pg 5). This is elucidated by the idea that any female in a larger group has a lower probability of being targeted by another female, because a female in a smaller group has a higher proportion of individuals above her, there are less options for the high ranked individuals to target. Thus the negative attention is concentrated in a smaller group. In the same way, a female's stress is related to the proportion of females that dominate her. In recalling the factors that influence stress from the introduction: lack of predictability, lack of control, lack of available outlets of aggression, interpretation of the events, lack of social support, increased risk of predation, less accessibility to food, and higher incidence of unprovoked aggression, it is found that higher incidence of injury suggests most of these factors. The variables that high injury incidence does not necessarily support, such as lack of social networks, and less resource accessibility could be explained by the factor of sociality in infant survival. Social isolation and low rank are correlated with lower infant survival in a highly social species such as the yellow baboon. Silk (2007) found that strong social bonds among female members of a group enhance infant chances but the direct reasons why were yet unclear. It may be partially explained by the practice of females forming friendships with males. These long-term friendships are used by the female to counteract male aggression that leads to infanticide (Nguyen et al., 2009).

Though these results seem to also suggest that a female's stress is also dependent on group size, the conclusions that we may draw from the effect of proportional rank on stress do not precisely allow this. In another study, group size was found to affect stress in a way that supported the optimal group size theory (Markham et al., 2015). Females with the least amount of stress resided in groups of intermediate size and this indicated that groups that are too small have intergroup conflicts that cause stress, (a larger group may perhaps drive a smaller one from a desirable area, for example). In the same vein, groups that are too large have many intragroup conflicts (like depleting a desirable area of all the food very quickly) and these cause stress as well.

Other relationships found in the models confirm the relationships found in literature. The positive relationship between chronic basal glucocorticoid levels and age is strongly established by years of work. Older yellow baboons have higher GC levels than younger baboons, and this causes deleterious effects in the body (Sapolsky & Altmann, 1991). Age and rise of basal GC are generally discussed in conjunction with physiological and psychological stressors. These stressors include risk of injury and illness (Archie et al., 2012) and gradually declining rank and BMI (Altmann et al., 2010). These stressors tend to relate to each other as well. For example, lower BMI negatively affects ability to engage in aggressive behavior so maintaining rank becomes more difficult. The direct contribution of glucocorticoid to the detrimental effects related to aging is likely immunosuppression and inhibition of growth hormone (Sapolsky & Spencer, 1997).

The many hormonal changes that happen during pregnancy include an adverse effect on stress level (Nguyen et al., 2008). A pregnant female is vulnerable, at a much higher risk of predation, and must work harder at finding food (Archie et al., 2014). Though there is a large spike in GC during the months of pregnancy, this change is not a permanent and basal GC concentrations return to post-partum levels. (Gesquiere et al., 2008). In the same paper, other environmental pressures were demonstrated to affect GC concentration. Their analysis was much more focused on climactic changes as they act on female stress. Parameters including daily rainfall averages and monthly temperature reports were included, and their conclusions ultimately were that hot temperatures and the dry season were the most taxing on a female. This is explained by a dearth of available food and shelter resources during the dry season, and the increased energy investment imposed by hot temperatures. The models used in this project reproduced the results of their paper, and this confirmation of all the relationships in the literature gives support to the novel predictions that I suggest.

Future work on this project will add group size to the model in an effort to support the findings in Markham et al (2015). Further, the LOESS lines in the appendix imply that work in this project should be directed towards explanation of these better fitting curves. LOESS curves are locally estimated at each point and the statistical package provides a smooth resulting curve. One limitation of a GLMM is of course that the predictions are linear due to the intent to find directional estimated relationships between the mean of one population and another.

Another example of the limitation of the proportional rank explanation of stress is that the lowest female ranked in a group will have the same proportional rank if a female above her has a daughter. The female's rank will go from 13 out of 13 to 14 out of 14, for example, and thus 1.00 is an absorbing boundary for this relationship. This idea also helps to show that proportional rank in itself is not indicative of the effect of group size on stress. An additional implication is that the alpha female technically has more stress when she dominates a lower number of individuals. With this logic, a female ranked 1 out of 4 is not only lower ranked than a female ranked 1 over 20, but she is also more stressed presumably due to the lower number of individuals. This is not easily explained by the idea that there is a lower proportion of individuals who may attack since that chance is very low anyway, so future work would address this concern as well.

In all, my findings suggest that instead of ordinal rank, proportional rank may act as a better predictor of the costs and benefits of group living in Amboseli female baboons. They also provide support to the existing literature concerning the complicated relationship between rank and stress for different species of mammals. Further, these results may also point to an evolutionary backdrop for the results found in the Whitehall studies. If similar results were confirmed and synthesized across primate societies and genders (with any exceptions accounted for, of course), then we would perhaps have an evolutionary pattern to strongly confirm the fitness disadvantage of low social rank in humans.

Tables:

Table 1. Model 1. Fixed effect factors on log fGC concentrations. Including proportional rank, dry season (dry = 1 and wet = 0), hot temperatures (hot = 1 and cool = 0), pregnancy (pregnant female = 1 non pregnant = 0), and age. Significant p-value is bolded.

	Estimate	Std. Error	P-Value
Proportional rank	4.00e-02	1.297e-02	**0.002**
Dry season	3.06e-02	2.982e-03	<0.001
Hot temperature	2.90e-02	3.737e-03	<0.001
Pregnancy	8.54e-02	3.180e-03	<0.001
Age	1.19e-02	4.960e-04	<0.001

Table 2. Model 2 results containing the fixed effects ordinal rank, dry season, hot temperature, pregnancy and age. *Insignificant* P-value is bolded.

	Estimate	Standard Error	P-Value
Ordinal rank	6.47e-04	5.074e-04	**0.202**
Dry season	3.07e-02	2.983e-03	<0.001
Hot temperature	2.90e-02	3.740e-03	<0.001
Pregnancy	8.54e-02	3.183e-03	<0.001
Age	1.16e-02	5.002e-04	<0.001

Table 3. Model 3 results including fixed effects proportional rank, ordinal rank, dry season, hot temperature, pregnancy status, and age. *Insignificant* P-value is bolded.

	Estimate of Effect on log(fGC concentration)	Standard Error	P-Value
Proportional rank	4.97e-02	1.668e-02	0.003
Ordinal rank	-5.95e-04	6.550e-04	**0.368**
Dry season	3.06e-02	2.982e-03	<0.001
Hot temperature	2.91e-02	3.739e-03	<0.001
Pregnancy	8.53e-02	3.182e-03	<0.001
Age	1.21e-02	5.247e-04	<0.001

Figures:

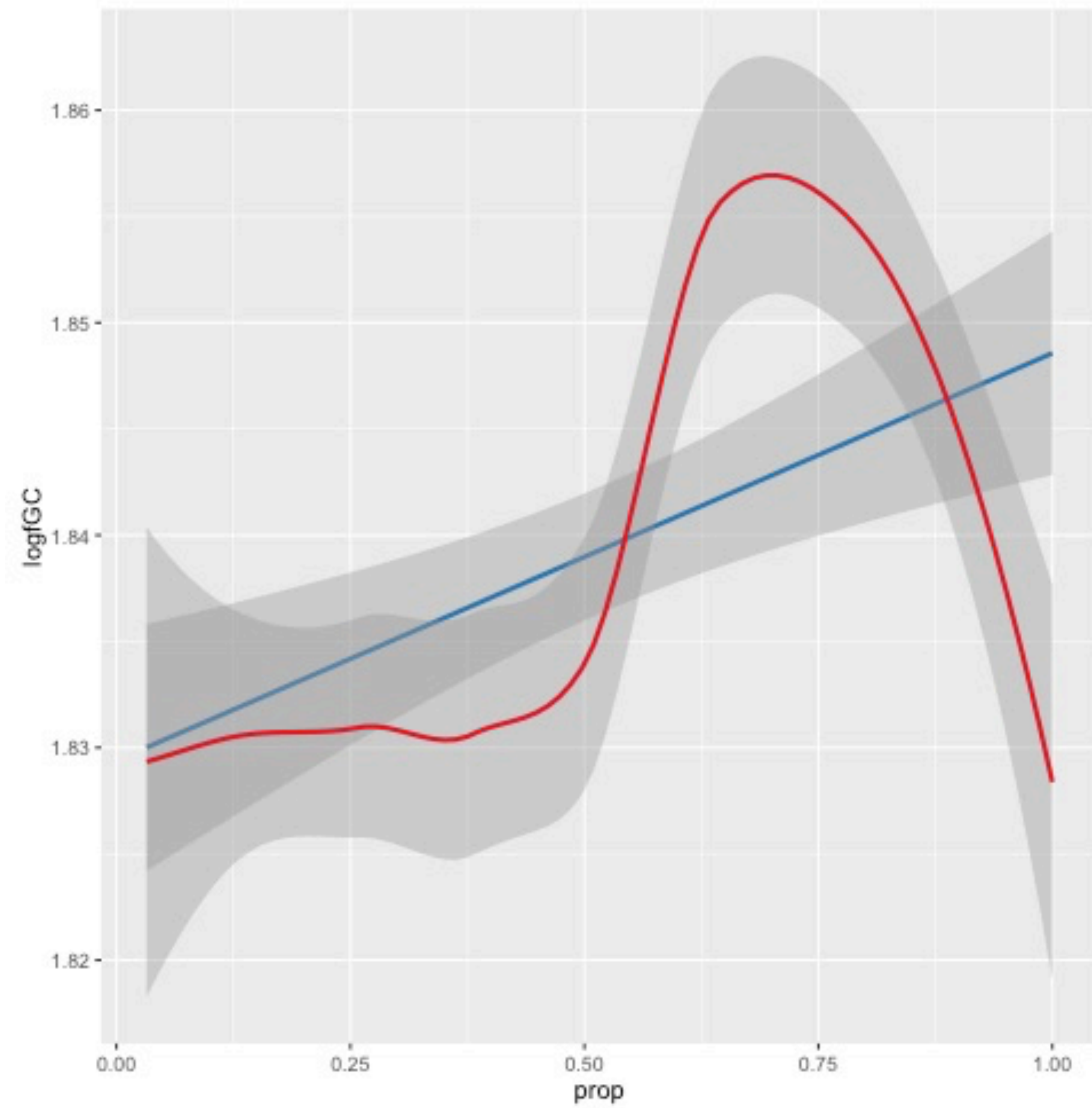

Fig.1 The effect of proportional rank on fGC concentrations, scatter plot points are removed for clarity. Linear estimate is in blue and LOESS estimate is red. fGC concentrations are in units of 1 nanogram/gram of dried feces

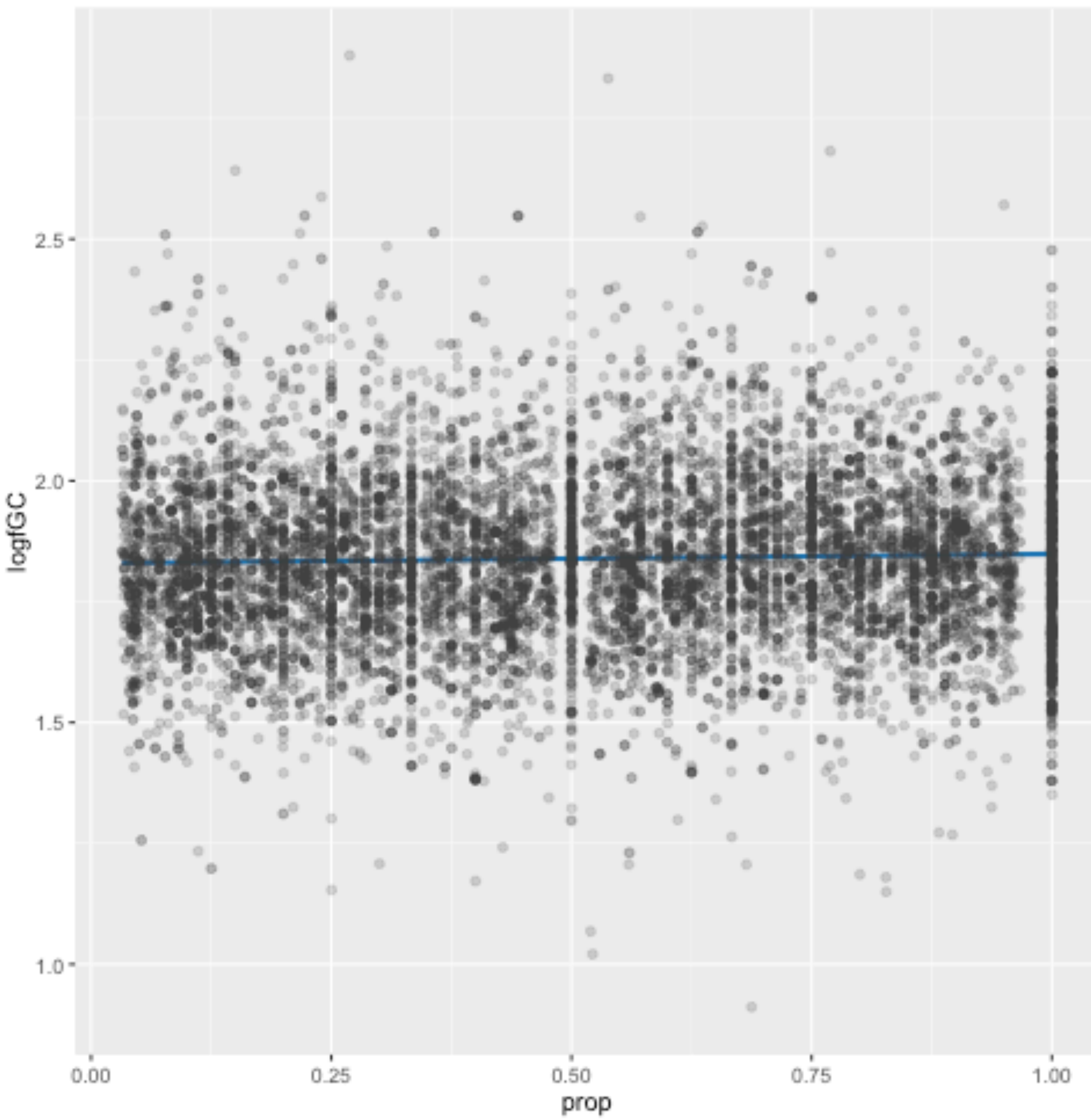

Fig 2. Scatterplot depicting the effect of proportional female rank on fGC concentrations. fGC concentrations are in units of 1 ng/g of dried feces.

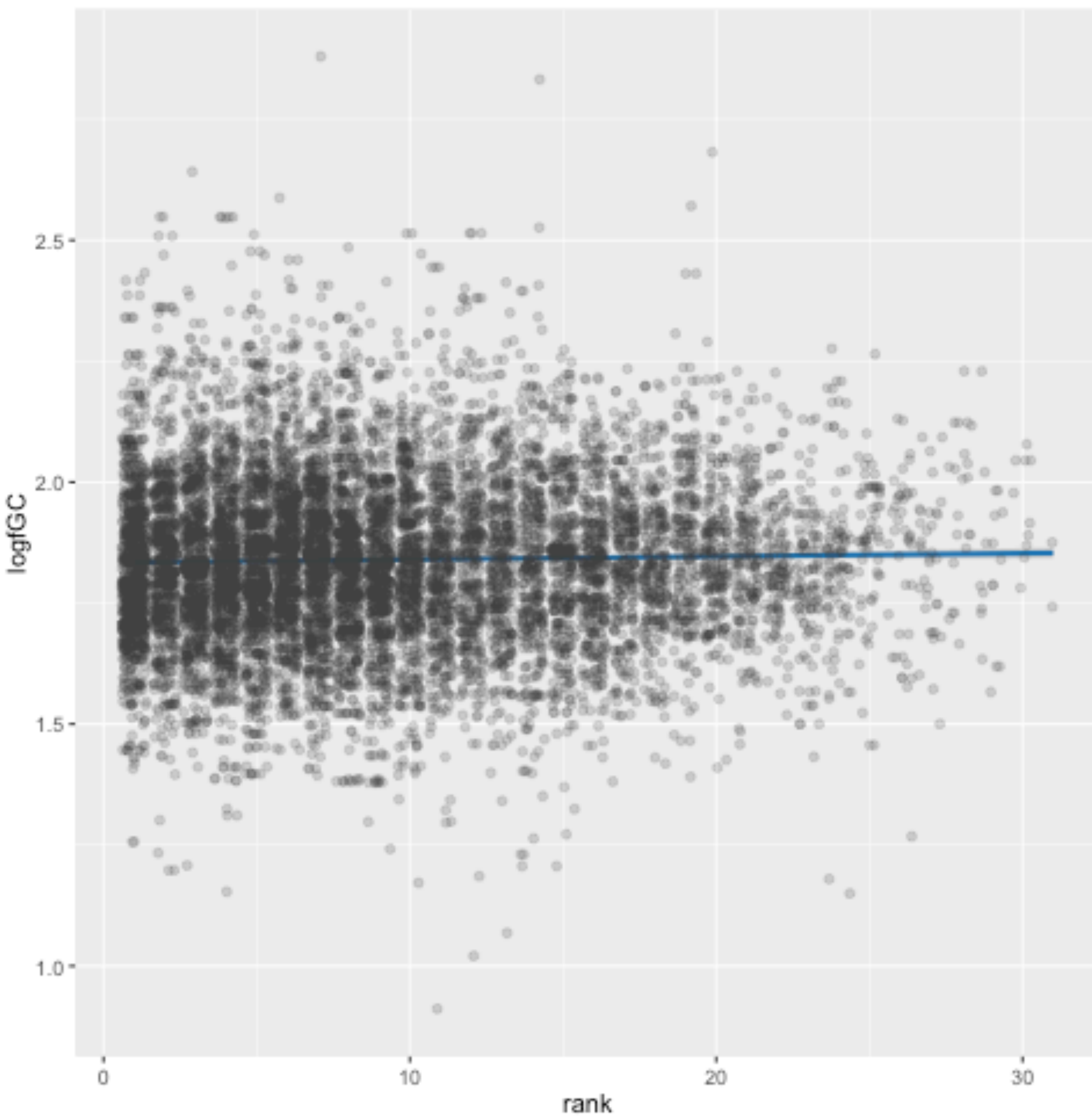

Fig 3. Scatterplot depicting the non-significant effect of ordinal female rank on fGC concentrations. fGC concentrations are in units of 1 ng/g of dried feces.

Fig 4. Correlation of fixed effects graphic shows pair-wise comparisons of each parameter of Model 3 based on Spearman's rank correlation coefficient. Proportional and ordinal rank's correlation is strongly evident. The intercept is log fGC. The relative magnitudes and directions of each effect on the others and on the intercept is graphically articulated through color intensity and size. Color denotes direction of relationship, with warmer colors indicating a negative effect and cooler colors indicating a positive one, size of circle indicates its relative effect.

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